

# FURTHER THOUGHTS ON DIOECISM AND ISLANDS<sup>1</sup>

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## ABSTRACT

Non-dioecious taxa are the floral majority, both in island floras and in those of the mainlands. This is true at all latitudes. Temperate zone islands have very low percentages of dioecious species. The percentages are somewhat higher in subtropical islands. Relatively high percentages of dioecism are found only in moist tropical islands or in floras that have had a moist tropical influence on their composition. Low islands in the tropics and rather arid islands in the sub-tropics and tropics have only small numbers of dioecious species in their floras. A multiple regression analysis shows that latitude and maximum height of islands together account for 82% of the variation in percentage of dioecism in our samples. Although autochthonous development of dioecism in an hermaphrodite immigrant cannot be ruled out yet, the percentage of dioecism in an island flora appears to be related to the percentage in a probable source flora in a comparable climatic zone. This equivalence could result from parallel evolution but probably depends more upon the long-distance dispersal, establishment, and radiation of taxa, including dioecious ones. This may be facilitated for the dioecious taxa by "leakage" in the dioecious breeding system, by dispersal of multiple-seed units, by longevity and vegetative propagation of perennial plants, and by an ability to utilize wind or unspecialized pollinators. In tropical regions, bird-dispersal of seeds particularly may have been involved in the stocking of forests on islands.

Lately, there has been increased interest in the breeding systems of seed plants and, more recently, this has been concerned with the role of dioecism in the origin and maintenance of adaptation to various environmental conditions (Ornduff, 1966; H. G. Baker, 1976; Freeman et al., 1976, 1980; Lloyd & Webb, 1977; Webb, 1979; Willson, 1979, 1982; Bawa, 1980, 1982; Bawa & Beach, 1981; Beach, 1981; Givnish, 1980, 1982; Lloyd, 1980, 1982; Cox, 1981, 1982, 1983; Thomson & Barrett, 1981; Ross, 1982).

Among these considerations has been the significance of dioecism in those flowering plants that make up the floras of islands (Bawa, 1980, 1982). Traditionally, it was temperate floras whose reproductive biology was studied, but as more attention is being given to islands in warmer climes, it is important that we do not go too far in the other direction and assume that tropical islands are typical of islands in general.

There is no difficulty in spotting dioecism or monoecism in wind-pollinated temperate zone trees and herbs, for the morphological differences between staminate and pistillate inflorescences are striking, being related to the very different functions of casting pollen into the wind and sieving pollen out from an aerial suspension, re-

spectively. But making a quick diagnosis of the breeding system is not so easy with insect-pollinated species, particularly in the tropics. Because both staminate and pistillate flowers must attract the same visitors, they tend to be similar in appearance, sometimes even to the extent of having pistillate flowers that produce non-functional pollen grains (e.g., *Actinidia chinensis*, Schmid, 1978; *Solanum* spp., Anderson, 1979).

Some of the difficulty that this has produced in attempts to quantify the occurrence of dioecism in tropical floras is shown by estimates of dioecism in the Hawaiian flora. Carlquist (1965) judged it to be 27.7% while Gilmartin (1968), basing her analysis on the flora written by Hillebrand (1888), reported it to be only 5%—a striking discrepancy. Both authors claimed not to include gynodioecious and other deviant species in the percentage. Possibly the truth lies somewhere between these extremes, but we use the Carlquist figure because Gilmartin, herself, suggested that Hillebrand (1888) may have had difficulty in identifying dioecism from imperfectly preserved specimens or rarely collected species. Also, Carlquist (1965) made studies of many species and did not rely solely on the literature.

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TABLE 1. Percentages of Dioecism in Islands and Corresponding Mainlands.

Category	Island	Number of Species	% Dioe- cism	Comparable Mainland	Number of Species	% Dioe- cism
Cool temperate	Iceland	472	3	British Isles	1,489	3
Warm temperate	Azores	391	2	Portugal	2,183	2
	Bermuda	136	4	Carolinas	3,274	4
	San Clemente	221	2	California	3,727	3
	San Nicolas	92	6			
Subtropical	Guadalupe	116	3	Baja California	2,564	3
	Juan Fernandez	141	11			
	Norfolk Island	153	12			
	New Zealand	1,800	13			
Subtropical Dry	Easter	30	0			
Tropical Dry	Galápagos	439	3			
Tropical Low	Bikini Atoll	44	2			
	Leeward Islands	40	0			
	Aldabra	171	4			
	Chagos Arch.	71	1			
Tropical High Indian Ocean	{ Réunion	838	4			
	{ Mauritius	682	11			
	{ Seychelles	237	8			
Pacific Ocean	{ Tonga	404	16			
	{ Guam	279	13			
	{ Samoa	539	17			
	{ Hawaii	1,467	28			

DIOECISM AND ISLAND COLONIZATION

In a thoughtful and thought-provoking paper, Bawa (1982) suggested that “dioecious taxa may have been disproportionately more successful in colonizing the (Hawaiian) islands.” This would seem to be out of accord with what Stebbins (1957) called “Baker’s Law”—that taxa that successfully establish seed-reproducing populations after long-distance dispersal will usually be self-compatible (or apomictic) and, by implication, show relatively low levels of inbreeding depression following self-pollination (H. G. Baker, 1955, 1967). A convenient assumption in the past has been that the original colonists of isolated islands will have been hermaphrodites or monoecious and their dioecious descendants developed outcrossing breeding systems autochthonously (that is, after arrival on the island) (H. G. Baker, 1967; Carlquist, 1965, 1966, 1974; Gilmartin, 1968). However, Bawa (1982) and others have pruned the list of genera in which dioecism is most likely to have arisen after the Hawaiian islands had been colonized by hermaphroditic plants, by pointing to the existence of dioecious species in

some of these genera outside of Hawaii. The subject is also discussed by Godley (1979) for the New Zealand flora.

Clearly, though, selection for outcrossing on islands could favor the evolution of dioecism since dioecism is more easily evolved than a functional self-incompatibility system. Mere alteration of the hormone system in a plant can produce separate staminate or pistillate flowers even on the same shoot (as in monoecious plants) without genetical difference. Consequently in the simplest case, dioecism could result through only a few genetic changes.

We believe that there is merit in considering the floras of a wider selection of islands than just the favorites—Hawaii and New Zealand. We have made use of floras written by specialists on the islands in question and have analyzed their species lists, with a special emphasis on “oceanic” islands that probably had no connection with a mainland since the origin of angiosperms.

We have been up against some difficulties because some published floras are little more than check-lists and, to some extent, it has been nec-



essary to take the condition of a species elsewhere as indicative of its sexual condition in the flora in question. Even less satisfactory is the need to judge, in other cases, simply on the known characteristics of the genus. We have taken care to consider only species that are native to each particular island, thereby excluding human introductions that are especially numerous on such islands as Bermuda and other relatively densely populated places.

Monocots and dicots were treated separately in our analyses but their subtotals are combined here for an overall representation of the proportions of hermaphrodite and monoecious versus dioecious species in each flora. Hermaphrodite and monoecious species are lumped because the point at issue is the potentiality, or lack of it, for self-pollination—and monoecious plants have this to almost the same extent as do hermaphrodites. Hermaphroditic species, in these calculations, mean not only those species that have so-called “perfect” flowers, but also those in which hermaphroditic flowers are accompanied by staminate flowers (andromonoecism), by pistillate flowers (gynomonoecism) or a mixture of all three (polygamy). Even gynodioecious and androdioecious species are counted in with the hermaphrodites, the criterion being that the populations include at least some plants that can function both as pollen-donors and ovule-producers. This is in contrast to the species that are regularly dioecious. Needless to say, the uncertainties are greater for little-studied tropical islands than for those that are extra-tropical and well known. But, despite some inaccuracies because of restricted information, we feel that the statistics that have emerged are probably accurate enough for the genesis of some conclusions.

There exists an estimate of the proportion of dioecious species in the world, published in 1922 by Yampolsky and Yampolsky. This is very useful as a standard for comparison with local floras even though, as Bawa (1980) has pointed out, it is probably an underestimate because of the underrepresentation of tropical species in this venerable compilation. But it is most unlikely that anyone else will undertake the Sisyphean labor of producing an updated version, so, with our fingers crossed, we can use the 3–4% that the Yampolskys decided upon as a minimal estimate of the proportion of dioecious flowering plants in the world. All investigators are agreed that there is a positive partial correlation of dioecism with a woody habit (e.g., Bawa, 1980; Givnish,

1982), and this means that floras rich in trees and shrubs will tend to have a higher percentage of dioecious species.

#### ISLAND FLORAS

##### TEMPERATE ZONES

The temperate zone islands whose published floras we have analyzed (Table 1) are those of cool temperate Iceland (Löve, 1970) and the warm temperate Azores (Watson, 1870), Bermuda (Britton, 1918), San Clemente (Raven, 1963), and San Nicolas (Foreman, 1967). The last two islands are situated in the Pacific Ocean off the coast of California. Available lists of mainland floras that can be compared with these oceanic areas are, respectively, those of Great Britain (Clapham et al., 1962), Portugal (Pires de Lima, 1947), the Carolinas (Conn et al., 1980), and California (Jepson, 1928; Munz, 1963). We quote the number of species for California from Jepson (1928) but found the same percentage of dioecism by analyzing the flora by Munz (1963).

We find that the proportions of dioecious species (Table 1) are no greater on the islands than they are on the mainlands and they are as low as Yampolsky and Yampolsky's (1922) world standard.

##### SUBTROPICS

Although the tropics are delimited by the Tropic of Cancer in the northern hemisphere and the Tropic of Capricorn in the southern hemisphere, there is no convenient boundary for the subtropics. Consequently, our categorization of Guadalupe Island (Eastwood, 1929), off the coast of Baja California, as subtropical and the exclusion of San Clemente and San Nicolas Islands as warm-temperate is somewhat arbitrary. In this connection, it is notable that the percentage of dioecious species in the flora of Guadalupe does not show any difference from those of the temperate zones and Guadalupe has the same percentage of dioecious species as the Baja California mainland (Wiggins, 1980). The Juan Fernandez islands, off the coast of Chile, are also sub-tropical, although with tropical floristic affinities (Skottsberg, 1922a, 1922b, 1928b). Here, with 11%, there is a definite suggestion of increase in the percentage of dioecism.

New Zealand is difficult to categorize because of its wide latitudinal range, and, even though it is largely temperate in climate, many of its floristic affinities are with the more tropical islands



to the north. This may have some responsibility for the rather large proportion of dioecious species in its flora (Godley, 1979) for, as we shall see, tropical islands that are large and mountainous are clearly richer in dioecious species than those of temperate regions.

Norfolk Island is interesting because it represents a sub-tropical island whose flora is probably derived from the same sources as the tropical or subtropical elements of the New Zealand flora, and, although the flora of Norfolk Island (Maiden, 1904) is smaller in number of species than that of New Zealand, its proportion of dioecious species is comparable—12%.

#### TROPICAL HIGH ISLANDS

In the tropics, floras of the islands that have mountains bearing moist forests have relatively high percentages of dioecious species (Table 1). This is shown by the floras of Samoa (Setchell, 1924; Christophersen, 1935, 1938), Hawaii (Hillebrand, 1888; Carlquist, 1965), Tonga (Yuncker, 1959), and Guam (Stone, 1970) in the Pacific Ocean and the Seychelles (Summerhayes, 1926), and Mauritius (J. G. Baker, 1877) in the Indian Ocean. Only the flora of Réunion (Cordemoy, 1895) in the Indian Ocean gives a surprisingly low percentage (4%).

However, this result for Réunion only accentuates an apparent slight difference between the percentages for the sampled islands of the Pacific and Indian Oceans, respectively. It may be that dioecious percentages are genuinely higher in Pacific Islands than in those of the Indian Ocean. This should be examined further and an attempt should be made to see if an explanation is to be found in the composition of the source floras or in the flyways of migratory birds. It has been suggested that other islands in the Indian Ocean east of Madagascar serve not as destinations but rather as "safety nets" for vagrant birds (Renvoise, 1971; Penny, 1971). Another possible explanation for the low proportion of dioecism in Réunion may be a relative overabundance of groups such as orchids and grasses which are rarely dioecious.

#### TROPICAL LOW ISLANDS

Unlike the high, forested islands, there are many small islands in the Pacific and Indian Oceans that are topographically low, and, in these islands, such as Aldabra (Hemsley et al., 1919), the Chagos archipelago (Willis & Gardiner, 1931),

Bikini atoll (Taylor, 1950), and the Leeward Islands of the Hawaiian archipelago (Christophersen & Caum, 1931), the largest proportion of the flowering plant species occupy the littoral and strand zones. There is a striking lack of dioecious species on these islands (Table 1) and the same is probably true for the strand and littoral floras of high islands that also have interior forests (Long in Gilmartin, 1968).

The flora of the Aldabra islands, in the Indian Ocean, has been studied more completely than most low islands (Fosberg, 1971; Renvoise, 1971, 1975; Woodell, 1979; Wickens, 1979) and its relationships to the bird fauna have been commented upon by Renvoise (1971, 1975) and Woodell (1979). These authors agree that the littoral flora of Aldabra had probably arrived by rafting whereas the inland flora had been introduced by stray birds or fruit bats. Penny (1971) has noted that Aldabra is not a wintering ground for any migrant waders (which, anyway, would not be likely to be important agents of inland fruit and seed distribution).

#### TROPICAL AND SUBTROPICAL DRY ISLANDS

The Galápagos are discussed separately here because they are relatively dry for tropical "high" islands. Their flora (Wiggins & Porter, 1971) shows a very low percentage of dioecism. It is notable that Rick (1966) performed a series of bagging and pollination experiments on 18 species with hermaphrodite flowers in the Galápagos and found no evidence of self-incompatibility, suggesting that outbreeding mechanisms are not strongly represented in the Galápagos flora.

Easter Island, being extremely isolated at a distance of 2,300 miles from the coast of Chile, has a very small indigenous flora (Skottsberg, 1928a), even though it reaches a height of 1,969 feet (600 meters). The climate is subtropical, and, because of its volcanic rocks and steep slopes, the landscape of Easter Island is arid (Skottsberg, 1928a), so it qualifies as a subtropical counterpart to the tropical Galápagos islands. The flora is predominantly herbaceous. Of the 30 angiosperm species present, none is dioecious; this is in agreement with our results for the Galápagos.

#### TROPICAL WOODY FLORAS

The only analysis of a complete tropical mainland flora that we have for comparison with those of the islands is that by Croat (1978, 1979) for Barro Colorado Island, which, prior to the flood-



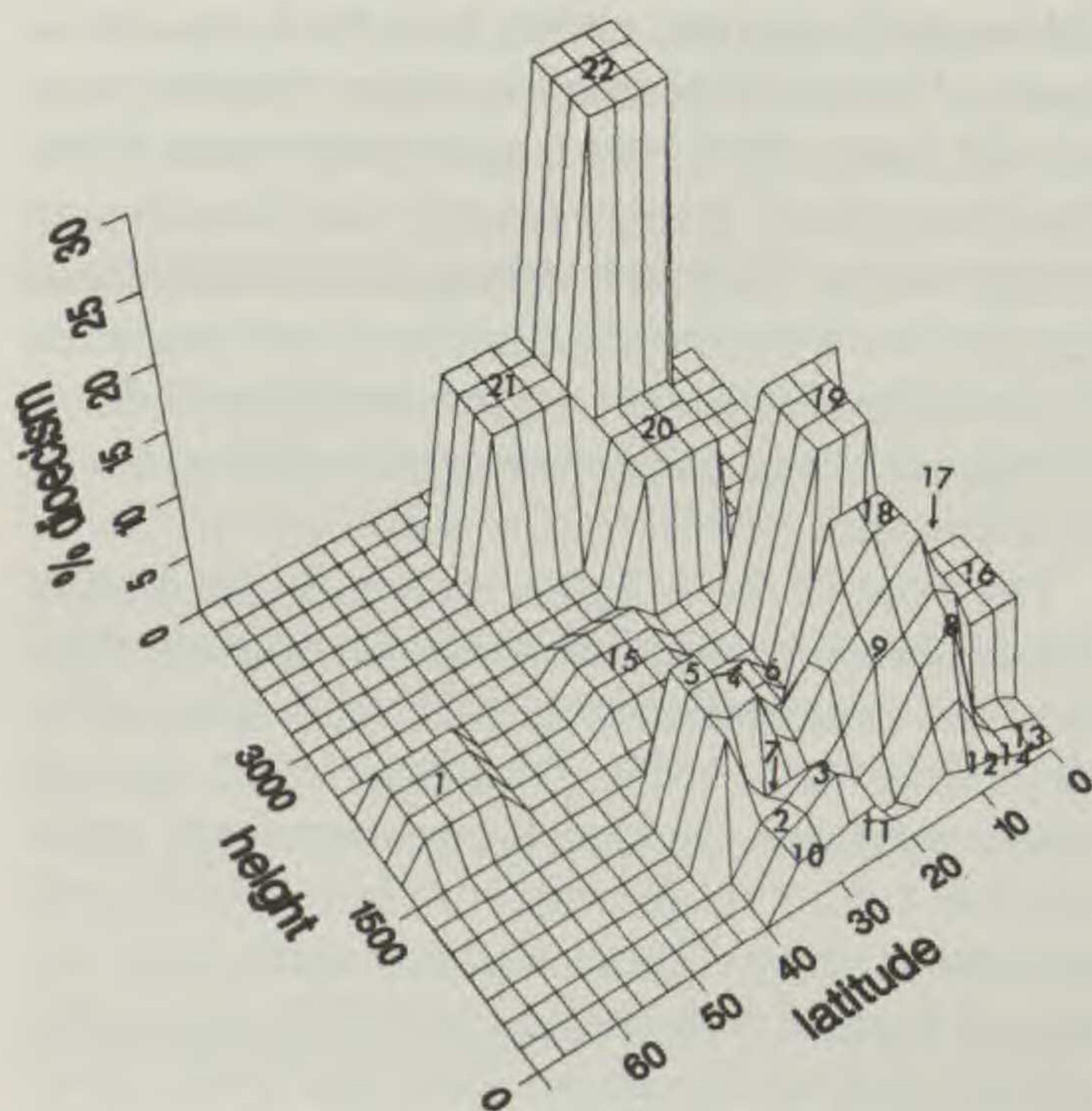


FIGURE 1. Graphical representation of percentage of dioecious angiosperms in island floras plotted against island height in meters and distance from the equator measured in degrees latitude for 22 different archipelagos or islands: (1) Iceland, (2) San Nicolas, (3) San Clemente, (4) Norfolk, (5) Juan Fernandez, (6) Guadalupe (Pacific Ocean), (7) Easter Island, (8) Guam, (9) Mauritius, (10) Bermuda, (11) Leeward Islands (Hawaii), (12) Bikini, (13) Aldabra, (14) Chagos archipelago, (15) Azores, (16) Seychelles, (17) Galápagos, (18) Tonga, (19) Samoa, (20) Réunion, (21) New Zealand, and (22) Hawaii.

ing of the Panama Canal from 1911 to 1914, was part of the mainland. Croat's (1979) calculation is that there are 9% of dioecious species in the Barro Colorado flora. Other calculations have been made for forest floras (in most cases just the trees) in mainland areas and they are summarized in Bawa (1980). Sobrevila and Arroyo (1982) have recently contributed a Venezuelan example. Percentages vary from 20 to 37%. This suggests that the tropical island forest floras have been derived from mainland sources that show a high percentage of dioecious species as Bawa (1982) and Givnish (1982) have already pointed out.

#### CORRELATIONS WITH ISLAND HEIGHT AND LATITUDE

The relationship between maximum island height and distance from the equator with the proportion of dioecious species can be seen in Figure 1. Through the use of multiple linear regression, we find that 82% of the variation in levels of dioecism between islands can be ex-

plained solely on the basis of maximum height of the island and its distance from the equator (as expressed in degrees of latitude) (Table 2). For the regression, percentage data were first transformed with an angular transformation ( $\theta = \arcsin \sqrt{p}$ , where  $p$  is the percentage expressed in decimal form). An analysis of variance of the regression indicates the regression to be very highly significant ( $P$  is very much less than 0.001), and  $F$  statistics computed for both partial coefficients of the regression show them to differ significantly from 0 (Table 2).

It is our belief that part of the remaining variation (18%) can be explained by the differing amounts of precipitation in the islands, but since this variable is not clearly independent of island height or latitude, nor is it uniform from year to year, we have not used it in our multiple regression.

#### DISCUSSION

In the 22 island floras we have studied, two important features are apparent: (1) the percentages of dioecious species in these islands do not generally differ from those in latitudinally comparable mainland floras, and (2) there is a very strong correlation between the level of dioecism and both the maximum island height and proximity to the equator.

Thus the contrast in the tropics between the low islands (and the dry islands), on the one hand, and the high forested islands, on the other, is clearly shown in statistics in Table 1 and in graphical form in Figure 1. This is very likely related to differences in the derivation of their floras from tropical mainland sources; that is, forests for high islands versus littoral vegetation for low islands. Island height may be thought of as a simple index of the potential habitat diversity of islands, particularly in the tropics.

Therefore, it is worth examining possible reasons why dioecism appears not to be such an impediment to the colonization of islands as might have been thought.

First, there may be the evolution of dioecism in a taxon that arrived at the island in the form of a self-compatible hermaphrodite. Carlquist (1974) listed 14 genera of flowering plants that appeared to be dioecious in Hawaii but are hermaphroditic or monoecious elsewhere. Bawa (1982) has pointed out that subsequent research has demonstrated that ten of these 14 genera are actually dioecious in certain non-Hawaiian locations as well. This, in itself, does not prove



TABLE 2. Analysis of Variance of Multiple Regression. Regression equation is:  $\theta = 12.6 + 0.0036(\text{height}) - 0.123(\text{latitude})$  ( $\theta = \arcsin \sqrt{p}$  where  $p = \% \text{ dioecism in decimal form}$ ). Percentage of variation in transformed data explained by multiple regression =  $1 - (50.3/274.8) = 82\%$ . Both partial regression coefficients are significant at the 0.01 level.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Regression	2	$\Sigma z^2 = 4,815.5$	2,407.5	47.8***
Deviations	19	$\Sigma d^2 = 956.27$	50.3	
Total	21	5,771.8	274.8	

that they have not evolved dioecism autochthonously in Hawaii, for they have demonstrated the genetic capability of becoming dioecious and could do so more than once. And there are still four genera (*Hedyotis* and *Canthium* in the Rubiaceae, *Santalum* in the Santalaceae, and *Wikstroemia* in the Thymelaeaceae) that may have developed dioecism only in the Hawaiian islands. There are also five endemic genera that are dioecious (Carlquist, 1974) and these could have developed dioecism in Hawaii (*Bobea* and *Straussia* in the Rubiaceae, *Broussaisia* in the Saxifragaceae, *Labordia* in the Loganiaceae, and *Touchardia* in the Urticaceae). So autochthonous evolution of dioecism cannot be ruled out entirely yet.

But it does seem that we should also be willing to allow that dioecious species can colonize islands in something like the same proportion that they show in mainland situations. And we need to explain why this is possible if they seem to need to be cross-pollinated to start the development of a seed-reproducing population. One possibility is that dioecism is not perfect in these species. Clearly, gynodioecious taxa should not be classed as dioecious, but it is also true that many taxa considered to be truly dioecious have occasional flowers of the opposite sex or of a hermaphrodite structure. Thus, there is the possibility of occasional seed setting, probably by self-pollination, in these taxa—especially as we know that in those cases that have been examined experimentally, hermaphroditic flowers in dioecious species are self-compatible (Baker, unpubl. data). This phenomenon, which we term "leaky dioecism," is the condition that prevails where hermaphroditism or bisexuality occurs at low levels in populations of otherwise dioecious species.

An example of leaky dioecism is found in Samoan populations of *Freycinetia reineckeii*, a liana of the Pandanaceae. Traditionally, the Pandana-

ceae have been believed to be a classic case of a dioecious family (Hutchinson, 1973). However, a recent examination (Cox, 1981) of populations of *F. reineckeii* in Western Samoa has revealed a consistent low level of bisexual plants (at levels ranging from 4 to 9%). The bisexual inflorescences borne by these plants produce viable pollen and also set fruit.

Working in the Philippines, B. Stone has also found a similar condition in *Freycinetia negrosensis* (see Cox, 1981), and Cammerloher (1923) noted it also in *F. strobilacea* in Indonesia. An *F. scandens* individual grown in the Royal Botanical Gardens in Sydney, Australia, from a single seedling from northern Queensland has been observed to produce staminate and pistillate spikes at the same time (Cox & B. Webster, unpubl. data). Although these levels of bisexuality may be low enough to be missed in herbarium studies, they may have been an important factor in the colonization of numerous isolated islands by the 190 species of this genus.

Other striking examples of leaky dioecism occur in the rubiaceous genus *Coprosma*. In the Juan Fernandez islands, Skottsberg (1922b) found a number of bisexual flowers on a branch of pistillate *Coprosma triflora*. In New Zealand, Godley (1979) reported hermaphrodite flowers on staminate plants of *C. robusta*. Fosberg (1937) reported pistillate inflorescences on a staminate bush of *C. cookei*, endemic to Rapa Island. A *C. pumila* bush growing in the University of California Botanical Garden in Berkeley produced some hermaphrodite flowers (Baker, unpubl. data).

Also in *Charpentiera* (Amaranthaceae) there is leaky dioecism (Sohmer, 1972). *Sanctambrosia* (Caryophyllaceae) is recorded as having leaky dioecism in the Desventuras Islands (Skottsberg, 1963). *Fragaria chiloensis* occasionally produces hermaphrodite flowers throughout its range along the Pacific Coast and the offshore islands of North



and South America. Also, *F. chilensis* is a hermaphrodite in Hawaii (Staudt, 1962).

Other examples of leaky dioecism occurring in New Zealand that have been noted by Godley (1979) include species in the genera *Cotula* (Compositae), *Clematis* (Ranunculaceae), *Pittosporum* (Pittosporaceae), *Dodonaea* (Sapindaceae), *Alectryon* (Sapindaceae), *Anisotome* (Umbelliferae), and *Astelia* (Liliaceae). *Fuchsia procumbens* has been made to produce seeds on staminate plants by hormonal treatments (Godley, 1979) and drought stress can result in the development of staminate flowers among the pistillate flowers in monoecious *Zea mays* (Moss & Downey, 1971). This listing could be greatly extended.

The late George Gillett, who knew the Hawaiian flora intimately, once said that he doubted whether there were any perfectly dioecious species in Hawaii—that there was always the possibility of an occasional seed being set by an abnormal flower on a staminate or pistillate plant.

Although it is not an island species, *Carica papaya* is an instructive example of a species with leaky dioecism (H. G. Baker, 1976). Staminate trees of this species are heterogametic as far as sex-determination is concerned (Storey, 1958, 1967). Consequently, when a staminate tree forms an occasional hermaphroditic flower that can be self-pollinated, the seeds produce plants of both sexes in the next generation. Thus, by leaky dioecism the dioecious condition is rederived from a single plant.

Another possible factor in the establishment of dioecious taxa after long-range dispersal is environmentally induced sex-lability, which has been demonstrated in several flowering plant genera (Freeman et al., 1976, 1980). It may be that on islands as well as mainlands, variations in environmental factors may trigger a change in sexual expression, resulting in the production of both pollen and eggs within an individual or a clone.

Another mechanism that might overcome the apparent disadvantage faced by a dioecious taxon upon arriving on an island by a single act of dispersal is the dispersal of multi-propagule units rather than single seeds (also mentioned by Wickens, 1979). Thus, more than one plant can be produced from a single immigration event. This is particularly likely to be the case with endozootic dispersal by birds of the seeds in berry fruits (which by definition are many-seeded).

It is notable that both Bawa (1980, 1982) and Givnish (1982) have drawn attention to the prevalence of endozootic dispersal of tropical forest tree seeds and have linked endozootic bird-dispersal of seeds with dioecism. They have suggested that potential dispersers will be more attracted to the greater fruit display that a pistillate tree can provide compared with the more resource-limited display of trees with hermaphrodite flowers and have proposed that the primary vectors of tree seed-dispersal to high tropical islands are such frugivores.

We simply bring these ideas together with the suggestion that endozootic dispersal, which promotes the defecation of several seeds as a group, could occasionally be effective in bringing staminate trees and pistillate trees onto islands in close proximity both in time and space. Thus, a seed-reproductive colony could develop. Although we believe that there is an abundance of multi-seed fruits in the tropics, it is notable that Flores and Schemske (1983) have shown an exceptional abundance of drupes in Puerto Rico. However, although drupes by definition are derived from a single, simple or compound pistil, they are not always one-seeded. A good example of a multi-seeded drupe is provided by the fruits of species of *Spondias* (Anacardiaceae).

Incidentally, endozootic dispersal is not the only mechanism by which multi-propagule units of dioecious taxa can be dispersed. For example, Lloyd (1972) has found in the genus *Cotula* in New Zealand that the achenes of these composites are dispersed individually in the monoecious species, but in the dioecious species the entire head may be dispersed as a unit.

In this regard, evolution may have gone either way in any particular taxon. Thus, either dioecious species may have been selected for fleshy fruitedness or fleshy-fruited taxa may have been selected for dioecism. In any event, the correlation is the same.

As a side-light, it may be noted that dioecism has been linked with multi-propagule units in plants other than angiosperms. Thus, Schuster (1966) noted that the four spores resulting from meiosis remain united as a tetrad in almost all of the dioecious bryophytes, and this tetrad, rather than the individual spore, becomes the unit of dispersal. Because each tetrad in the dioecious taxa contains two "male" and two "female" spores, male and female gametophytes can develop in proximity to each other.



Another factor that mitigates the potentially deleterious effects of dioecism is a woody, perennial, iteroparous habit, often associated with strong powers of vegetative propagation (Bawa, 1980). Thus, a single plant of a dioecious species on an island may simply "wait" for the advent of a propagule of the opposite sex to grow to maturity nearby.

One has only to think of the Canadian pondweed, *Elodea canadensis*, which invaded Europe during the nineteenth century and succeeded in blocking waterways by purely vegetative production of ramets even though probably only a female plant was introduced (Clapham et al., 1962). An island example of this phenomenon can be seen on San Clemente Island, in the Pacific Ocean off the California coast. A single pistillate bush of *Baccharis viminea* was noted in 1900 by Trask (1904) and was still there when Raven (1963) saw it, although it had grown considerably during the interval. To the best of our knowledge it still remains there, although we hope that its lonely vigil has since been rewarded by the arrival of a staminate plant. Certainly it can continue to wait for a long time, in our human scale, but such a delay in the advent of a reproductive partner may not be long on the evolutionary time scale.

The picture of pollination biology on moist, high tropical islands appears to be in accord with another idea proposed by Bawa, who suggested (Bawa, 1980, 1982; Bawa & Opler, 1975) that many dioecious species in the tropics have flowers that are adapted to visitation by small generalist insects, particularly small bees and flies.

Because potential insect pollinator faunas on oceanic islands are frequently depauperate in number of species (Carlquist, 1974), and the insects are believed to be unspecialized in their choice of flowers to visit, dioecious plant species that do not require specialized pollinators may have a greater chance of establishment than those plants that require a specialized kind of visitor. Linsley et al. (1966) have shown that a high proportion of Galápagos plants are pollinated by a single carpenter bee (*Xylocopa darwini*). Similarly, Woodell (1979) has demonstrated that a corresponding role is played on Aldabra by a beetle (*Maucoleopsis aldabrensis*).

This advantage of unspecialized pollination systems is not limited to entomophilous taxa, but occurs also in dioecious taxa with vertebrate pollination. Thus, the genus *Freycinetia*, which

is widespread throughout the islands of the Pacific, is pollinated by a variety of opportunistic, non-coevolved vertebrates that range from large flying foxes and starlings to small white-eyes and endemic honeycreepers in Hawaii (Cox, 1982, 1983). A variety of bats, birds, and rodents has been recorded as visitors to the genus *Freycinetia* in various other places in the South Pacific (Cox, 1982).

Another case of unspecialized vertebrate pollination in dioecious taxa might be seen in the epiphyte genus *Collospermum* (Liliaceae), which may be pollinated by the endemic sheath-tailed bat in New Zealand (Daniel, 1976), but which is probably pollinated by a variety of other bats, birds, and possibly insects in other islands in the South Pacific.

All of these considerations that we have made have been directed to the demonstration that island floras usually bear a close resemblance in the percentage of dioecism to the mainland floras, from which they have been derived more or less by long-distance dispersal. And, if the mainland flora is a forest flora with a high proportion of dioecious taxa, it can be reproduced on the island without serious violation of Baker's Law. But we should be less than circumspect if we did not draw attention to another area in which investigation is needed. This is related to studies of the breeding systems of trees in dry and wet forests in Costa Rica (Bawa, 1974; Bawa & Opler, 1975) that have shown that a high proportion of the hermaphrodite-flowered tree species are self-incompatible. A similar result is reported from Venezuela (Sobrevila & Arroyo, 1982).

Is this picture of high levels of self-incompatibility also reproduced in the forests of large, high, moist tropical islands? Until the necessary experimental work is done, we cannot know. But, Godley (1979) and Pandey (1979a, 1979b) agree that while dioecism is strongly represented in the New Zealand flora, self-incompatibility appears to be rather rare, and we note the negative results of tests for self-incompatibility in the drier Galápagos flora conducted by Rick (1966).

However, there have been a few indications of self-incompatibility in the Hawaiian flora, e.g., *Plantago grayana* (Tessene as quoted in Carlquist, 1970), and we must wait for further experiments to show if we need to invoke "leaky self-incompatibility" as well as "leaky dioecism" to account for plant breeding systems in the islands!



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